

CHAPTER 6-1

LIMITING FACTORS AND LIMITS OF TOLERANCE

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Figure 1. Janice Glime overlooking geothermal vents that stretch the limits of tolerance of bryophytes. Photo by Zen Iwatsuki, with permission.

Sad, faint, and weary, on the sand
Our traveller sat him down; his hand
Cover'd his burning head.
Above, beneath, behind, around,
No resting for the eye he found;
All nature see'd as dead.

One tiny tuft of Moss alone
Mantling with freshest green a stone
Fix'd his delighted gaze;
Through bursting tears of joy he smiled.
And while he raised the tendril wild,
His lips o'flow'd with praise.

O! shall not He who keeps thee green,
Here in the waste, unknown, unseen,
Thy fellow-exile save?
He who commands the dew to feed
Thy gentle flower, can surely lead
Me from a scorching grave.

Pushing the Limits

Crum (2004) quotes from Stark (1860, Popular History of British Mosses) concerning the tiny tuft of *Fissidens* that Mungo Park found in the African interior. Park wrote "I considered my fate as certain, and that I had no alternative but to lie down and perish." Just as Park was giving up, he spied the tiny moss.

So many have failed to see the tenacity with which the bryophytes hold on to life. Their limits of tolerance seem to outrange any other group in the Kingdom Plantae. But the mechanisms by which they do this have remained obscure to the average biologist, and even to most physiologists. Yet they have much to teach us about basic principles of physics and chemistry applied to living organisms to create their physiological processes.

When I began my studies of bryophytes, I did so because no one could answer my questions. It seemed as if we knew almost nothing about them. There was in fact a wonderful literature, mostly from other countries, that I discovered later and that none of my professors (not

bryologists) had ever read. Nevertheless, the mysteries of how bryophytes survived where they did continued to intrigue me, and most answers seemed nowhere to be found in the published literature. Then I became interested in *Fontinalis* and began to question just what determined which streams would have it and which did not. Soon I was testing it to its limits, trying to ascertain why it seemed unable to occur in certain parts of the world and only in certain streams in other parts. In fact, my friends soon began asking, if I liked *Fontinalis* so much, why was I always trying to kill it? I was testing its limits of tolerance.

Bryophytes have unique physiologies that are often envied by the horticulturalists and agriculturists. Their ability as a group to survive cold and desiccation is unparalleled by any other major group of plants. It is these physiological abilities that permit them to occupy bizarre habitats like iron stoves (Figure 2) and darkened caves, geothermal vents and meltwaters (from snow and ice), and only a liverwort was able to survive on the first samples of moon rock.



Figure 2. Old iron stove with bryophytes growing on it. Photo by Janice Glimme.

The tolerance of bryophytes for conditions that would impose severe stress on other members of the kingdom led a group of astrophysicists at a special session on space colonization at the 40th American Institute of Aeronautics and Astronautics (AIAA) Aerospace Sciences Meeting, held in Reno, Nevada, 14-17 January 2002, to suggest that these organisms should be introduced to the moon for **terraforming** (making desert planet etc. habitable; Davis 2002). (Never mind the arguments as to which celestial body should be colonized first.) Indeed, based on their importance in Earth's polar and alpine **ecosystems** (communities & habitat) where most flowering plants are unable to survive, it was suggested that following preparation by the microbial stage, it is the bryophytes that would be able to transform the planet/moon into a habitable body. But, the scientists advised, further research is needed to improve our understanding of the physiological and ecological roles these organisms might play in such a system. Do they realize how little we know of their role on Earth?

Our understanding of bryophyte physiology is at best poor. Compared to tracheophytes, bryophytes have enjoyed few physiological studies, and many assumptions

have been made about their physiology. Perhaps the most widespread and erroneous assumption was that all bryophytes have the same sort of basic physiological mechanisms for obtaining water and nutrients, and for retaining them or losing them. Implicit in this was the assumption that all gained water and nutrients from leaf surfaces. However, recent studies on bryophyte physiology suggest that physiological mechanisms may be the most variable character among different populations and species of bryophytes. While tracheophytes were spending their genetic evolution on morphological adaptations to environmental conditions, it seems that bryophytes may have been spending theirs perfecting a multitude of physiological and biochemical strategies. Before we delve into the physiology itself, we will begin with a discussion of our understanding of stress factors and plants as they might apply to bryophytes.

C-S-R Triangle

In 1976, Stearns reviewed the concepts of life strategy or life history tactic to help explain a system of co-evolved adaptive traits that permit species to survive in a range of habitats, and these concepts have subsequently become known as **life cycle strategies** or **life history strategies**. Numerous papers exist arguing pros and cons of using the term *strategy* for a non-thinking, non-planning plant, but the term conjures up the appropriate concepts in our thinking and I can think of no other that does quite as satisfactory a job, so the term strategy has become part of my own ecological jargon as it has likewise in ecological literature.

While Stearns (1976) was developing the life strategy concepts, Grime (1977) took a slightly different approach and suggested that external factors that limit plant **biomass** (living & dead plants or plant parts) may be classified as either stress or disturbance. Following this concept, **stress** refers to those conditions that restrict production, such as low light, insufficient water or nutrients, or suboptimal temperature. **Disturbance** is the partial or total destruction of the plant biomass arising from herbivores, pathogens, humans, wind damage, frost, desiccation, erosion, or fire. (It seems that pollution belongs there too!) Plants respond to these limiting factors with three types of strategies: **stress-tolerant**, **ruderal**, and **competitive** (Table 1), reminiscent of Ramensky's (1938) **patients** (stress-tolerant), **explerents** (ruderal – growing in wastes or among rubbish), and **violents** (competitive), which will be discussed in more detail with growth forms (During 1992). Using Grime's (1977) scheme, individual species of plants, therefore, represent compromises between the conflicting selection pressures of competition, stress, and disturbance. These relationships can be arranged in a triangle known as the **C-S-R model** (Figure 3). Grime (1979) considers it highly unlikely that plants can tolerate extremes of both stress and disturbance. Some, however, might be able to tolerate each independently.

Table 1. Grime's (1977) suggested basis for the evolution of three strategies in tracheophytes.

Intensity of Disturbance	Intensity of Stress	
	Low	High
Low	competitive strategy	stress-tolerant strategy
High	ruderal strategy	no viable strategy

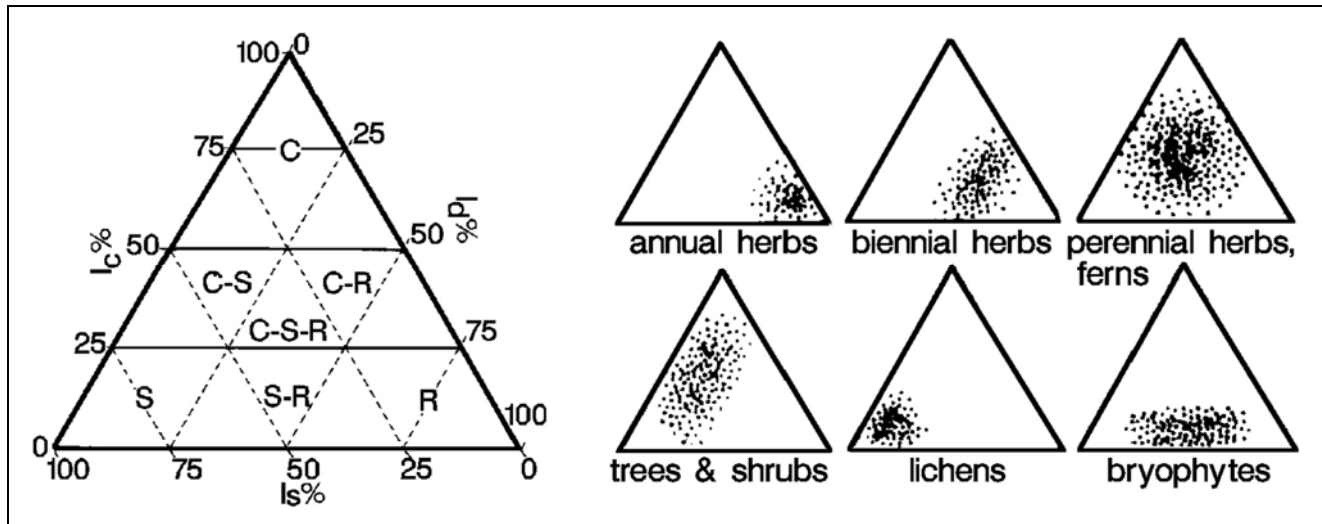


Figure 3. **Left:** Model of equilibria between competition, stress, and disturbance in plants, showing relative importance (I_c , I_s , I_d). Strategies include competitors (**C**), stress-tolerators (**S**), and ruderals (**R**). **Right:** Diagrams of the strategy ranges of various groups of plants compared to the distribution of competitors, stress-tolerators, and ruderals. Redrawn from Grime (1977).

Grime (1974) proceeds to define **competition** as "the tendency of neighboring plants to utilize the same quantum of light, ion of a mineral nutrient, molecule of water, or volume of space." **Stress**, in Grime's usage, encompasses "the external constraints which limit the rate of dry matter production of all or part of the vegetation."

Competitors tend to have moderate to long life spans, relatively low reproductive efforts, high potential relative growth rates, high dense canopies of leaves, abundant litter, and high morphological plasticity. The plant forms are diverse, including perennial herbs, shrubs, and trees. This strategy generally does not fit the bryophytes due to their relatively slow growth rate. In fact, Grime and coworkers (1990) concluded that none of the bryophytes in their study have a competitive strategy. Rather, they are stress tolerators. Their lack of a "sophisticated" transport system renders them unable to monopolize resources and dominate the vegetation of an undisturbed ecosystem. It is only in aquatic habitats, particularly streams and bogs/poor fens, where they may be able to compete with tracheophytes due to their perennial above-substrate persistence. Nevertheless, competition with such life cycle stages as seedlings is real, with deep mats of bryophytes suspending the young plants where they either are unable to reach the earth to anchor their roots or are unable to reach the light to obtain energy. And competition among bryophytes occurs, although on such a slow, yet dynamic scale that it has seldom been documented. Competition as a strategy will be discussed later.

Stress tolerators similarly have a long life span and low reproductive effort, but they have low potential relative growth rates, little but persistent litter, and little morphological plasticity. The plant forms are most diverse, including such distant ones as lichens, bryophytes, and trees. Among the bryophytes, one advantage is that they are able to reproduce asexually by fragmentation when stress may be too severe for gametes, embryos, or sporogenous tissues to survive.

Ruderals are more like competitors, but they have very short life spans and high reproductive rates. They are mostly ephemerals that tend to have relatively

homogeneous life histories and habitats. Flood plain bryophytes can be considered here (Figure 4).



Figure 4. The floating liverwort *Riccia fluitans* stranded above water as it would be following a flood. It will form a broader thallus on land. Photo by Jan-Peter Frahm, with permission.

Severe Stress

With their inability to move when living conditions become stressful, plants must have plasticity to survive. For most plants, diversity is maintained through the second set of genetic information, available when conditions change, and permitting the next generation to benefit from whatever combination is appropriate. Although self-fertility is usually prevented within flowers, fern gametophytes, and moss branches, it often is not prevented between flowers of the same plant and certainly not among flowers of the same clone; the same seems to be true in bryophytes, although much less evidence supports this contention.

Such genetic diversity, the product of outcrossing (breeding with a different population or genetically different individual), would seem only to benefit plants when they must cope with long-term changes, those that last over the course of several years, decades, or millennia. A different method of coping must be available for those

stresses that are encountered within the course of a single growing year as a result of seasonal changes. Low-level stress is undoubtedly present in all habitats and functions merely as a modifier of growth rates and competition, whereas severe stress, such as coping with winter, has an immediate impact on the survival of the organism (Grime 1977). Not only can severe stress eliminate a species from a habitat directly, but it can also eliminate a species indirectly by reducing its competitive ability, making it vulnerable to replacement by more stress-tolerant species. Strategies of growth thus must respond to seasonal variation in temperature, nutrient, and moisture supplies, a concept consistent with the life-form definition of Mägdefrau (1982). Grime and coworkers (1990) found a functional specialization in the life cycle of bryophytes, with a different set of strategies for the established (adult) phase than those being used in the regenerative (juvenile) phase, thus providing one means for coping with seasonal changes.

The **relative growth rate (RGR)** of a species is generally considered the best measure of the success of the species relative to other individuals or species in a given environment. Furness and Grime (1982) found that RGR for bryophyte species could be correlated with stress conditions in laboratory experiments. For the short-lived ruderal *Funaria hygrometrica* (Figure 5), $\text{RGR} = \text{ca. } 50 \text{ mg g}^{-1} \text{ day}^{-1}$, and for the competitive *Brachythecium rutabulum* (Figure 6), $\text{RGR} = 70 \text{ mg g}^{-1} \text{ d}^{-1}$. By contrast, stressed bryophytes such as **epilithic** (living on rock) species had much lower productivity ($\text{RGR} = 5\text{--}20 \text{ mg g}^{-1} \text{ d}^{-1}$). Since tracheophyte RGR ranges from 4 to $400 \text{ mg g}^{-1} \text{ d}^{-1}$ (Poorter & Remkes 1990), it seems that bryophytes are on the low end of the scale, and if Furness and Grime are right in their conclusion that low RGR relates to stress tolerance, bryophytes in general should be particularly good at it.



Figure 5. The short-lived ruderal species, *Funaria hygrometrica*, illustrating its high reproductive rate. Photo by Michael Lüth, with permission.

Grime (1977) considered four types of environments that impose severe stress. He regarded the arctic-alpine and arid habitats to have low production, with stress being imposed primarily by the environment. In shaded habitats, stress is plant induced, and for bryophytes, this causes a release of competition from less tolerant tracheophytes, giving bryophytes an advantage. In nutrient-deficient

habitats, bryophytes can often again dominate due to lack of tracheophyte competition. To these stressful habitats, I would add the habitats with extremes of high mineral loading, very high or very low pH, or high temperatures. Polluted environments can present any or all of these conditions, as can geothermal fields (Figure 1).



Figure 6. The competitive species *Brachythecium rutabulum*. Photo by Janice Glime.

Bryophytes, as a group, tend to be wide-ranging in this scheme, with their center of distribution being in the stress-tolerant ruderals (During 1992). Økland (1990) considered even the mosses in a Norwegian mire to be stress tolerators. He made this judgment because they occurred in dry, shaded sites, relative to those of *Sphagnum*, and by their narrow habitat niches within the mire. These were generally bryophytes with wide niches in other vegetation types. It seems that bryophytes in general are stress tolerators, relegated to living where other taxa are unable to survive.

Genetic Adaptations

The ability of a plant to tolerate a condition is dependent upon three factors: genetic components, currently interacting factors, and past history. Shaw (1987) used *Funaria hygrometrica* (Figure 5) to illustrate the effect of pretreatment (past history) versus genetics on tolerance to zinc and copper for protonema growth and stem production. For that species, the protonema growth responded to past history, but for the stem production, genetic differences were more important. Furthermore, genetic differences between populations were more important than pretreatment. Such results suggest the possibility of selection as a result of past history in the genetically different populations.

Genetic drift (random changes in gene frequencies due to isolation of a small population) can also account for differences between populations in widely separated areas. I (Glime 1987) found vastly different growth rates between the populations of *Fontinalis novae-angliae* (Figure 7) from New Hampshire and Michigan when they were grown in a common garden. Vitt *et al.* (1993) found that *Scorpidium scorpioides* (Figure 8) from Canada grew best in extreme-rich fen waters, whereas plants from The Netherlands grew best in water from moderate-rich fens and in nutrient-enhanced conditions. Either of these cases could represent genetic drift, but both could also represent past history (*e.g.* physiological acclimation) or natural selection. For the *S. scorpioides*, past history may well play a role because both

populations grew best in water of the type from which they had been collected, suggesting that at least it is possible that osmotic relationships of the existing cells may have been affected by the change in water chemistry.



Figure 7. *Fontinalis novae-angliae* growing on rock at edge of stream. Photo by Janice Glime.



Figure 8. *Scorpidium scorpioides* growing in a fen. Photo by Michael Lüth, with permission.

One significant mechanism that permits plants to respond to stresses in a short period of time is by production of **inducible proteins** (proteins produced only when certain conditions are present) (Wray 1992), a genetically controlled phenomenon, but also potentially a result of past history. Such production is mitigated by inducible enzymes that respond to environmental cues such as toxic metals, salts, anaerobic conditions, temperature extremes, pathogens, and nutrient availability. Others respond secondarily to internal hormonal cues such as ABA (abscisic acid), ethylene, and GA (gibberellic acid). These hormonal mechanisms would appear to be available to the bryophytes, since all of these hormones are known in bryophytes. Inducible proteins are less well known among the bryophytes, but may some day prove to be important in their success. We are already gathering considerable information on stress proteins that respond to dehydrating conditions and high temperatures, as will be discussed when we examine water relations. Furthermore, Grime and coworkers (1990) contend that morphological plasticity is of reduced importance for bryophytes in exploiting disturbed habitats. Rather, their dispersal and regeneration abilities permit them to occupy inaccessible and disturbed habitats such as cliffs, walls, and forest clearings.

We can conclude that genetic components, currently interacting factors, and past history can work together or

alone to elicit the responses we see in many bryophytes as they respond to stress.

Crystals – Adaptive?

Many new things appear due to mutations and developmental errors, but most of these fail to persist into a second generation. Some do persist, to the consternation of humans, with no apparent function. One such genetic invention may have been that of crystals formed by some mosses.

Jean Faubert (Bryonet 24 August 2010) reported a whitish substance under mosses in their fern greenhouse. Joselito Arocena (Bryonet 24 August 2010) suggested that this layer might be an accumulation of crystals of calcium oxalate, perhaps associated with mycorrhizal fungi, although Faubert did not find direct evidence of fungal presence. Such formations occur around roots of tree throws. Arocena *et al.* (2001) suggested that these crystals may protect fungal hyphae (*Piloderma fallax*) from desiccation and decrease the build up of calcium and oxalate in fungal cells. When associated with mosses, the formation of calcium oxalate may help them maintain their phosphorus supply and protect them from predators. The oxalate form could provide a reservoir during times of low calcium (Tuason & Arocena 2009). There is also an association between calcium oxalate and phosphorus, with more calcium oxalate crystals being formed under high levels of phosphorus.

Neil Bell (Bryonet 25 August 2010) reported that *Mniodendron colensoi* (= *Hypnodendron colensoi*; Figure 9), a moss in the preserved patches of Kauri forest on the North Island of New Zealand, has prominent crystals in the costae of leaves. Bryologists have assumed these to be calcium oxalate, but verification is needed.



Figure 9. *Mniodendron colensoi*, Bill Malcolm, with permission.

Jeffrey Duckett and Silvia Pressel (Bryonet 25 August 2010) used X-ray analysis to test fresh material from New Zealand and found abundant calcium but no other cations or anions. They therefore presumed that the substance was indeed calcium oxalate.

Do Nutrients Limit Bryophytes?

Those who culture bryophytes know what nutrients to manipulate and what nutrient levels may be too much. But we seem to know much less about the effects of nutrients in nature.

Wang *et al.* (2014) addressed this question in the cushion moss *Leucobryum juniperoideum* (Figure 10–Figure 12). In eastern China, this moss occurs only in certain habitats. The **epigeic** (ground-dwelling) populations (Figure 10) occur only in areas that have a moso bamboo (*Phyllostachys edulis*) forest. The **epixylous** (on logs lacking bark) (Figure 11) are restricted to areas with Chinese fir (*Cunninghamia lanceolata*) forest. **Epilithic** (rock-dwelling) populations (Figure 12), on the other hand, live in both of these habitats. N and P concentrations differed markedly between the epigeic and epixylous habitats, with soil concentrations of these nutrients being much higher in the latter. So why is this species restricted to logs in the *Cunninghamia* forests? In experiments, growth of *L. juniperoideum* was reduced by N additions of 0.1 mol L⁻¹ over six months. On the other hand, addition of up to 0.1 mol L⁻¹ P caused growth increase. Furthermore, high concentrations of N (200 mg L⁻¹) significantly reduce germination rates and delay early development from spores. P, on the other hand, has no such negative effects. Thus, high soil concentrations of N are limiting in the distribution of this species.



Figure 10. *Leucobryum juniperoideum* on soil. Photo by David T. Holyoak, with permission.



Figure 11. *Leucobryum juniperoideum* on log. Photo by Jan-Peter Frahm, with permission.



Figure 12. *Leucobryum juniperoideum* on a rocky substrate. Photo by Li Zhang, with permission.

Summary

Some bryophytes are able to live in bizarre habitats like iron stoves, deep caves, and glacial surfaces. These habitats test the limits of tolerance of the species. The high tolerances of some bryophytes led a group of aerospace scientists to suggest that bryophytes should be used for **terraforming** on the moon.

Bryophytes have evolved a variety of life cycle strategies for coping with the wide diversity and seasonal changes in their earthly habitats. Grime categorized plants by their limiting factors into **stress-tolerant**, **ruderal**, and **competitive** (**C-S-R model**), similar to Ramensky's **patients**, **explerents**, and **violents**, respectively. Compared to other plants, bryophytes fall along the bottom of the C-S-R triangle as non-competitors but with many stress tolerants and ruderals.

The **relative growth rate (RGR)** serves as a good measure of the success of a species. The ability of the species to tolerate its conditions and have a healthy growth rate is dependent upon genetic components, currently interacting factors, and past history. Genetic drift and physiological responses to the environment help to make populations look different.

Inducible proteins are able to respond to changes in the environment, thus permitting the plant to behave differently under different environmental circumstances.

Many adaptive mechanisms elude us, while others may have no modern function at all. Incorporation of calcium oxalate is one of those factors that thus far has escaped our understanding.

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